SZENT-IVANY, J. J. H. & J. H. BARRETT. 1956. Some insect pests of banana in the territory of Papua and New Guinea. Papua New Guinea Agr. J. 11:1–5.
VANE-WRIGHT, R. I. 1971. The systematics of *Drusillopsis* Oberthur (Satyrinae) and the supposed amathusiid *Bigaena* van Eecke (Lepidoptera: Nymphalidae), with some observations on Batesian mimicry. Trans. Roy. Entomol. Soc. Lond. 123:97–123.

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# CHARLES REMINGTON'S CONTRIBUTIONS TO THE SPECIES CONCEPT

**Additional key words:** speciation, hybridization, hybrid zones.

The following remarks were written with the encouragement of the Editor in order to supplement issue 49(4) of the *Journal*, which commemorated the career of Charles Remington. I first met Charles Remington in 1971 at the Pacific Slope meeting of our Society, at which he gave a talk on the special aspects of genetic divergence and speciation on islands. His presentation, as in his writing, was authoritative, detailed, liberally spiced with interesting non-lepidopteran examples, and delivered with conviction. Charles Remington has long held a special interest in speciation. No topic is more central to evolutionary theory, nor more controversial, and those with strong conviction soon themselves become controversial.

Remington was an early proponent and remains a strong advocate for the "Biological Species Concept" (BSC), wherein species are thought to arise by genetic divergence in isolated populations, and are defined by presumed (the usual case) or by demonstrated (less often) reproductive isolation from closely related taxa. Traits serving this isolation function are assumed to have evolved through, or were perfected by, selection favoring the reduction of wasteful interspecific hybridization. Early criticism of the BSC stressed the difficulty in demonstrating reproduction isolation, especially between allopatric populations of organisms not amenable to experimental hybridization. Indeed, the great majority of lepidopteran species and subspecies are based on comparisons of wing pattern and genitalia, not on demonstrated mating barriers or measured hybrid fitness. More recently, the "Recognition Concept" proposes that reproductive isolation is only an incidental byproduct of adaptations increasing reproductive success through the evolution of species-specific mate recognition systems. Hybrid zones would seem a likely setting to observe the perfection of incipient reproductive isolation, yet few convincing examples have been found among many detailed studies. The apparent long-term stability of hybrid zones conflicts with Remington's view that they should be ephemeral, quickly evolving toward either fusion or toward speciation and a cessation of hybridization (see Collins 1991 and Coyne 1994 for reviews of these controversies).

The divergence in allopatry tenet of the BSC has endured, partly because biogeographic patterns of variation support it, and also because population genetics theory shows that even low rates of gene flow can prevent divergence between adjacent populations. Remington's early papers cited intriguing patterns of phenotypic variation, and advocated the active pursuit of studies in geographic variation and speciation by lepidopterists (Remington 1951, 1958). The work of his graduate student Charles Oliver was a product of this period, in which Oliver hybridized intra- and interspecific populations to reveal geographic variation in genes controlling reproduction and development (Oliver 1972, 1978, 1979a, 1979b. 1980). These studies complemented allozyme surveys of variation in genes coding for protein synthesis, and showed that the genetic basis for hybrid incompatibility may first arise within a species as regional ecological adaptations. In spite of the fact that Lepidoptera are relatively easily collected and bred, few other studies of this type have been conducted.

Many natural hybrid zones are known in Lepidoptera, and Remington was among the first to recognize their importance as natural laboratories in which to study the genetics of speciation. His "suture zone" paper (Remington 1968a) is now considered a classic in which he provided examples among varied animal taxa of hybridization along well-defined zones. The geographic location of these zones, and concordant distribution among unrelated taxa, strongly support the model of secondary hybridization as a result of range expansion from Ice Age refugia.

Remington's unwavering support of the BSC may lie in the appeal of the explanatory power of the genetic mechanisms thought to promote the formation of species: genetic divergence in the absence of homogenizing gene flow; selection against wasteful hybridization upon secondary contact of such divergent populations; the origin of reproductive isolation; speciation accomplished. Remington has often referred to these processes as "sequelae," and his deterministic view of speciation is reflected in his title "Genetic differences in solutions to the crises of hybridization and competition in early sympatry" (Remington 1985). The current view of species, following two decades of applying molecular techniques of genetic analysis, reveals a pattern of uncoupled evolution among categories of traits. Premating isolation, postmating compatibility, morphological characters, and physiology may evolve at vastly different rates. Some very similar species can exist in sympatry (sibling species), and other distinctly different species may freely hybridize in the lab or along hybrid zones. Many animal species simply cannot be defined on the basis of effective reproductive isolation.

Remington has long advocated experimental hybridization as a means to understand speciation (Remington 1958). Ironically, in one of his few species descriptions, Remington (1968b) was unable to obtain critical test crosses between his *Papilio gothica* and *P. zelicaon*, and the former is now thought by some to be an example of seasonal polyphenism in the latter. Recent cladistic studies (e.g., in the frog genus *Rana*, Hillis 1988) have shown that measures of reproductive compatibility from experimental hybridization may not be concordant with phylogenetic relationships established on the basis of molecular and morphological traits. In these examples, those taxa that freely hybridize may not be as closely related as other pairs showing reproductive isolation. For this reason, and because hybridization can lead to reticulate (vs. branching) evolution, advocates of the phylogenetic species concept spurn experimental hybridization data in their analyses. Yet, as Remington has so forcefully stated, laboratory crosses are extremely useful in revealing differences among species for regulatory genes controlling reproduction and development (e.g., Collins 1984). The proper phylogenetic interpretation of hybrid data can be derived from independent cladistic studies using molecular and other character sets (Avise & Ball 1990). Unfortunately, with several notable exceptions (see Lorkovic 1985, Sperling 1987, Powell 1995, Scriber et al. 1996, Tuskes et al., 1996), too few multidisciplinary works have been done in Lepidoptera taxonomy. Let us hope that the new generation of workers, with their powerful molecular techniques, will read and be stimulated by Charles Remington's insightful writings.

## LITERATURE CITED

AVISE, J. C. & R. M. BALL. 1990. Principles of genealogical concordance in species concepts and biological taxonomy. Oxford Surv. Evol. Biol. 7:45–67.

COLLINS, M. M. 1984. Genetics and ecology of a hybrid zone in *Hyalophora* (Lepidoptera: Saturniidae). Univ. Calif. Press Ser. Entomol. 104:1–93.

———. 1991[93]. Speciation: a review of concepts and studies with special reference to the Lepidoptera. J. Res. Lepid. 30:45–81.

COYNE, J. 1994. Ernst Mayr and the origin of species. Evolution 48:19–30.

HILLIS, D. M. 1988. Systematics of the *Rana pipiens* complex: puzzle and paradigm. Ann. Rev. Ecol. Syst. 19:39–63.
LORKOVIC, Z. 1985. Enzyme electrophoresis and interspecific hybridization in Pieridae (Lepidoptera). J. Res. Lepid. 24:334–358.
OLIVER, C. G. 1972. Genetic and phenotypic differentiation and geographical distance in four species of Lepidoptera. Evolution 26:221–241.
———. 1978. Experimental hybridization between the nymphalid butterflies *Phyciodes tharos* and *P. montana*. Evolution 32:594–601.
———. 1979a. Genetic differentiation and hybrid viability within and between some Lepidoptera species. Am. Nat. 114:681–694.
———. 1979b. Experimental hybridization between *Phyciodes tharos* and *P. batesii* (Nymphalidae). J. Lepid. Soc. 33:6–20.
———. 1980. Phenotypic differentiation and hybrid breakdown within *Phyciodes "tharos"* (Lepidoptera: Nymphalidae) in the Northeastern United States. Ann. Entomol. Soc. Am. 73:715–721.
POWELL, J. A. (ED.) 1995. Biosystematic studies of conifer-feeding *Choristoneura* (Lepidoptera: Tortricidae) in the western United States. Univ. Calif. Publ. Entomol. 115:1–275.
REMINGTON, C. L. 1951. Geographic subspeciation in the Lepidoptera. Lepid. News 5:17–20.
———. 1958. Genetics of populations of Lepidoptera. Proc. 10th Intl. Congr. Entomol. 2:787–805.
———. 1968a. Suture zones of hybrid interaction between recently joined biotas. Evol. Biol. 2:321–428.
———. 1968b. A new sibling *Papilio* from the Rocky Mountains, with genetic and biological notes (Insecta, Lepidoptera). Postilla 119:1–40.
———. 1985. Genetical differences in solutions to the crises of hybridization and competition in early sympatry. Boll. Zool. 52:21–43.
SCRIBER, J. M., R. H. HAGEN & R. C. LEDERHOUSE. 1996. Genetics of mimicry in the tiger swallowtail butterflies, *Papilio glaucus* and *P. canadensis* (Lepidoptera: Papilionidae). Evolution 50:222–236.
SPERLING, F. A. H. 1987. Evolution of the *Papilio machaon* species group in western Canada (Lepidoptera: Papilionidae). Quaest. Entomol. 23:198–315.
TUSKES, P. M., J. P. TUTTLE & M. M. COLLINS. 1996. The wild silk moths of North America. Cornell Series in Arthropod Biology. Cornell Univ. Press, Ithaca, New York. 264 pp.

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## DONATION OF THE ATSUSHI KAWABE LEPIDOPTERA COLLECTION TO THE SMITHSONIAN INSTITUTION

**Additional key words:** *Archips*, Tortricidae, Japan, Taiwan, Thailand.

On 27 November 1993, Atsushi Kawabe, a leading authority on Japanese Tortricidae, passed away at the age of 57 in Tokyo, Japan. Mr. Kawabe was born on 10 January 1936 in Ishikawa Prefecture, and after 1955 he lived in Setagaya, Tokyo and Chiba Prefecture